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REACTIONS OF PARAMOECIUM CAUDATUM TO LIGHT

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The experiments of Engelmann, Jennings, and Mast have demonstrated that Paramoecium shows neither orienting nor directive responses to light. Mast (1911, p. 134), who has recently studied this question with care, makes the following statement: "At noon on a perfectly clear day in July I arranged a double convex lens 10 cm. in diameter so as to focus the direct rays from the sun on a slide under the microscope. The light was passed through distilled water in order to cut out the heat rays. The light at the focal point was at least 500,000 ca. m. in intensity. This extremely intense light was repeatedly flashed upon the Paramoecia as they swam about under the microscope, but there was no evidence of any response whatever. It is altogether probable, then, that the power to respond to light is not common to all protoplasm."

The above statement and that of Engelmann, that Paramoecium bursaria, a species containing chlorophyl, is positively responsive to decreases of light intensities only when the oxygen content of the water is below normal, have seemed to me to allow further work along the line of intensity reactions in Paramoecium. The investigations of Hertel (1904) and of Oettli (1910) have shown that Paramoecium is responsive to ultraviolet rays and to heat rays. Why may it not react to visible rays whose wave lengths are between those of ultra-violet and heat?

Apparently no work has been done on the activating effect of such light stimuli on the ciliary apparatus of Paramoecium, though much has been done on the directive and orienting effect of such stimuli. If different light intensities do cause an increase or decrease in the ciliary motion of Paramoecium, it might be exhibited in either of two ways, or by a combination of the two:—(1) by causing increased or decreased rapidity in the beating of the cilia, driving the animal along its normal spiral pathway at different rates of speed; (2) by widening or narrowing the curve of the spiral and hence decreasing or increasing the forward advance of the animal while the rate of motion is unchanged; or (3) by a combination of a change in the rapidity of the ciliary action and a change in the diameter of the spiral pathway. With the view of testing out these possibilities, the following investigations were undertaken under the direction of Dr. G. H. Parker, to whom the writer wishes to express his thanks and appreciation for the careful supervision of the results embodied in this article.

The animals used were all Paramoecium caudatum, obtained from sixteen different cultures, and kept under varying conditions of light. Individuals from three cultures that contained conjugating lines were used at the same time as those from non-conjugating lines, and careful records were kept to see if the physiological factor was in operation. Some cultures were kept in darkness for twelve hours preceding the trials, while other cultures were exposed to day light or electric light for the same period. The animals were placed in a hanging drop of water one-half inch in diameter and so arranged on the stage of the microscope that all light rays except those coming through the condenser were entirely excluded. The observations were conducted at a magnification of 25 diameters and camera tracings were carefully made of the paths of the animals during their exposure to the stimulus. The observations were all for a period of one-half minute and the traced paths were carefully measured with a planimeter. The stimulus consisted of a 32 c.p. Mazda bulb mounted on a sliding base and the intensities of the stimulus varied from 5 to 1422 candle-meters, gained by moving the light through the space between a point 15 cm. and another 250 cm. from the microscope. A cooling stage, through which cool distilled water was run, was used to prevent

heating. The experiments were carried on in a darkened room so that the only possible light rays were those from the electric light used to illuminate the animal.

The size of the hanging drop was such that the path of the animal was very free from the sudden swervings due to hitting the boundaries of the drop. At least one minute was always allowed, for the purpose of overcoming the mechanical stimulation due to the transfer of the animal to the hanging drop, before any measured observations were taken. Some series were made in which the maximum stimulus was the first used and then the intensities were gradually decreased until the minimum intensity was reached. Other series were run in the opposite direction, while a third set consisted in sudden jumps from one extreme intensity to the other. All records were made in a room in which the temperature was always between 21° and 22° C.

The experiments were first made with the object of measuring the possible effect of the various light intensities upon the width of the spiral pathway. Animals were placed either in water or in weak gelatin solutions, which slightly retarded their speed, and careful measurements of the widths of the spirals, under various intensities of light were made. There was no measurable difference in the width of the spirals, no matter what intensity of stimulus was used, but a measurable change in speed was found, which must have been due to a change of ciliary activity in response to a change in the stimulus. The greater the intensity of the light used, the faster the animal moved, hence the greater the ciliary activity.

The distances of the light from the hanging drop and the corresponding intensities of the light were as follows:—

Distance in cm......	15	25	50	75	100	125	150	175	200	125	250
Intensities in C. M..	1422	512	128	58	32	20.5	14.2	10.5	8	6.5	5.1

The average rate of speed of the animals in response to each intensity, irrespective of conditions preceding the trials as regards the light environment, and including animals from both conjugating and non-conjugating lines, was as follows:—

Intensities in C. M..	1422	512	128	58	32	20.5	14.2	10.5	8	6.5	5.1
Average velocity in cm. per min......	8	7.95	6.95	6.35	6	5	4.75	4.50	3.75	3.5	3

These averages are based on the results of 500 trials at each of the eleven intensities of light and contain the individual records that do not harmonize with the final conclusion, namely, that a higher intensity of light is accompanied with a higher rate of locomotion. In a series of 200 trials, animals were started under the highest intensity of light and carried through each intensity to the opposite extreme and back to the starting point. In a second test a similar course was run except that it started and ended with the lowest intensity of light. The results of these two series are shown in the form of curves of response in Fig. 1, in which the intensities are plotted as abscissae and the distances in centimeters per minute as ordinates.

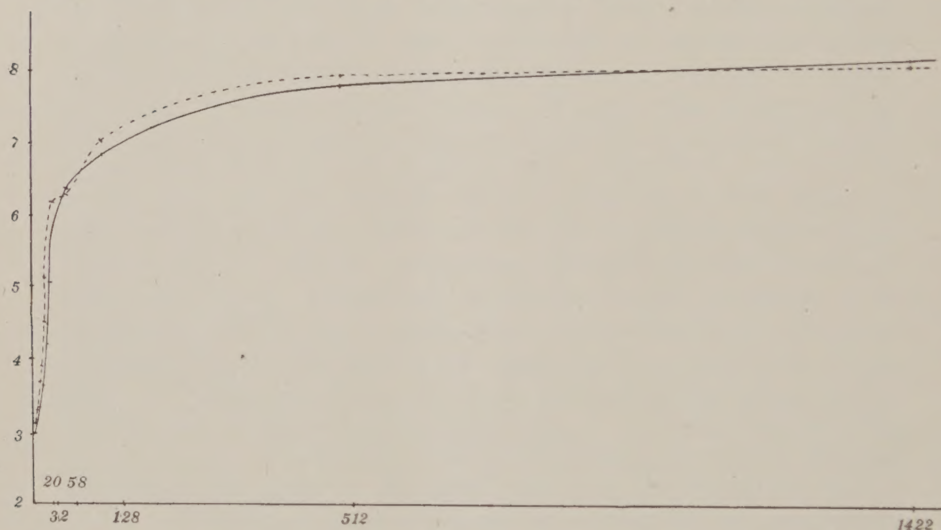

FIGURE 1

The heavy line represents the curve of response for the animals that began at the lowest intensities and the broken line that for animals which began at the highest intensities. These two curves practically coincide, thus showing, among other things, that the mechanical stimulation of placing the animal in the hanging drop did not cause an abnormal movement at the beginning of a series of trials.

Trials were also made in which the stimulus was changed suddenly from one extreme to the other. The response of the animals in such cases was different from that which the pre-

vious work had led me to expect. In the beginning no change in the response of the animal to the increase or decrease of the stimulus was observable. The rate at which the animal had been traveling before the change in stimulus was made, was continued, and this lasted sometimes for as long as two minutes after the change had been made. If, however, the new stimulus was maintained for a longer period, a change in the rate of locomotion was noted, and gradually the response became the one found to be normal for the given intensity of stimulus. This slowness of response to sudden changes of the light may perhaps account for the fact that former observers have not noted the increased speed of Paramoecium in response to an increase of the light stimulus.

Another curious fact was observed in the behavior of animals that were undergoing conjugation. In such cases about 40 per cent of the animals were entirely irresponsive, or only very slightly responsive, to any change in the intensity of the light stimulus. Often the difference in response was noticeable only when the records for the two extremes of intensities were compared. In non-conjugating lines only 10 per cent of the individuals were poorly responsive to changes in the intensity of the light.

In 2 per cent of the animals tested there was found negative, or rather inhibitory, response to increased light. The greater the intensity of the light, the slower the locomotion until at the upper limit (1422 C. M.) practically all movement ceased. The power of motion was slowly regained as the intensity of the light was decreased.

There were no differences found between the responses of the animals kept in daylight, in electric light, or in darkness for the twelve hours preceding an experiment.

Both fresh and stagnant water were used in order to ascertain whether the amount of oxygen present has any effect on the activity of Paramoecium, but no such effect could be detected.

Although the light was also used to illuminate certain portions of the field to a greater extent than other portions, there was absolutely no evidence in the motions of Paramoecium of a directive or an orienting effect of this unequal lighting.

The conclusions that I have been led to in this study of the reactions of Paramoecium in response to increases and decreases of the light are as follows:—

(1) In 55 per cent of the animals from conjugating lines and in 85 per cent of the animals from non-conjugating lines tested, there was increased rate of locomotion in response to increased light intensity.

(2) In 2 per cent of the animals tested the response to increased intensity indicated inhibitory influence; the greater the light intensity, the slower the locomotion.

(3) In 40 per cent of the animals from conjugating lines, there was no response, or at best a feeble one, to any change in the light intensity. This fact points towards the conclusion that the physiological state of Paramoecium at the time of conjugation is such that the threshhold of light stimulation is raised beyond the intensities used in these experiments.

(4) No evidence was found that the amount of light to which the animals had been exposed before the tests had any effect on the subsequent response to the stimulus.

(5) Responses to sudden changes of intensity in the light were only gradually effected.

(6) Paramoecium responds in essentially the same way to the same intensity of stimulus, irrespective of the previous intensity to which it has been exposed, provided only that it be given time to adjust itself to the new condition.

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A CRITICISM OF THE TROPISM THEORY OF JACQUES LOEB[1,2]

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CONTENTS

INTRODUCTION

There are two classes of biological investigators. One is concerned with *facts;* the theories which are based upon known facts serve him only to explain facts, to condense them into some general aspect, so that a deeper insight into the meaning of the whole problem may be gained. Even when his work lies along theoretical lines, to him facts are of the first importance. Should a fact be discovered which contradicts the theory, then the theory must suffer.

To the other kind of investigator the insignificant isolated facts are of no importance. His soaring mind desires universal recognition for the results of his achievement. The glittering *theory* is everything to him, the facts only its servant. If the fact does not suit, then it will be forced into the Procrustean

[1] The literature of the whole subject may be found in Loeb's paper: Die Tropismen, in Winterstein's Handbuch der vergl. Physiologie, Bd. 4, 1913.

[2] The original text of this paper is published in the *Biol. Centralblatt,* Bd. 35, Nr. 11, 1915.

bed of the theory or else so superficially studied that at first one is hardly aware of the discrepancy which lies deeper.

The crowning example of a theory which exerts such tyranny over facts is the so-called *tropism theory*, whose principal supporter is J. Loeb. To the criticism of this theory and, if possible, its refutation, the following pages are devoted.

The tropism theory has already been criticized by various writers (Jennings, Radl, etc.). They, however, always content themselves with pointing out that certain isolated cases do not harmonize with the theory. The most important general arguments have not yet been presented. Besides this, in his last publication in the Handbuch der vergleichenden Physiologie of Winterstein, 1913, Loeb shows that these criticisms have not affected him in the slightest degree, for he still reiterates the same opinions. For this reason a further investigation of the subject seems justified.

The word *tropism* denotes only a simple fact of observation. Many lower animals have the peculiarity of either creeping in a straight line away from or toward a source of energy, or a point from which light, heat, chemical energy, etc., radiates, or of choosing a path which is at right angles to the energy rays. These movements of orientation, which are also present in the lower plants, are termed *tropisms*, and are further known as photo-, chemo-, thermo-tropism, according to the kind of energy. Such lower animals can be drawn in a definite direction just as surely as a physicist can deflect a magnetic needle; and their behavior, giving so strongly the impression of being purely physical, has led the fathers of the tropism theory to regard the whole phenomenon as something very simple, whose solution may be found without any regard to the complicated structure of the organisms themselves.

To show how such an attempt has been made, the positive heliotropism of the winged aphid is cited, using Loeb's own words. He writes: "Two factors determine the progressive movement of animals under these conditions. One is *the symmetrical structure of the animal* and the second is *the photochemical action of the light*. * * *

The symmetrical structure of the animal is expressed anatomically in that, as is well known, the right and left body halves are symmetrical. But in my opinion, such symmetry exists not

only in an anatomical sense, but in a chemical sense; by which I mean that *symmetrical body regions are chemically identical* and have the same reactions, while *asymmetrical body regions are chemically different*, and in general have quantitatively or qualitatively different reactions. * * * If now more light falls on one retina than on the other, the chemical reactions also, for example the organic oxidations, will be more accelerated in one retina than in the other, and correspondingly greater chemical changes will occur in one optic nerve than in the other.

This inequality of the chemical processes spreads from the sensory to the motor nerves and finally to the muscles with which the latter are connected. We conclude from this that with an equal illumination of both retinas the symmetrical groups of muscles of both body halves are influenced chemically in the same way and so are in the same state of contraction; while, if the reaction speed is unequal, the symmetrical muscles on one side of the body are in greater activity than on the other side. The result of such unequal activity of the symmetrical muscles of both body halves is a change in the direction of the movement of the animal.

This alteration of the direction of the movement can either cause the head to turn toward the source of light, so that consequently the whole animal moves in the direction of the source of light; or else to turn the head in the opposite way and the animal moves in the opposite direction. * * * As soon as this has happened the two retinas are equally lighted and the (symmetrical)[3] muscles in both body halves once more work with the same strength. In consequence there is no longer any reason that the animal should deviate from this direction to one side or the other. It is therefore automatically led to the source of light. The will of the animal, which in this case dictates his direction, is the light, as it is gravity in the falling of a stone or the movement of the planets." (1909, pp. 9-14.)[4]

Jennings has aptly termed this theory, the "*theory of local actions*," because it does not regard tropism as a movement of the animal as a whole, but as a movement of both *body halves*, which work against each other. This we must remember as an

[3] Italics and (symmetrical) added by the present author.

[4] Loeb, Jacques. Die Bedeutung der Tropismen für die Psychologie. Vortrag gehalten auf dem VI. Internationalen Psychologenkongress zu Genf. 1909.

important characteristic of the tropism theory, and also, that in direct consequence of this, according to the theory, the turning of the animal must always be around an axis which lies in the plane of symmetry that separates the two body halves.

A second, perhaps even more important characteristic of the theory is the complete *disregard of special structure,* which simply does not exist for Loeb and his followers. We need know only that the organism is symmetrical,—the theory is just as applicable to protozoa or larvae of the simplest structure as to the most complicated Metazoa—and that the organism reacts to the particular energy; all else accounts for itself. Whoever reads Loeb's writings might readily conclude, from different expressions that are found here and there throughout, that he is fighting against the conception that regards the actions even of the lower animals as voluntary acts of the will, and *denies that they are involuntary.* This, of course, is not the case, and is meaningless. Involuntary action is an undeniable fact of observation, which expresses itself in the phenomenon that under definite conditions all individuals of a species do the same thing; no one questions the existence of involuntary action, even though he may hold the view that not all the actions of the lower animals are involuntary.

Loeb has rather set himself the task of explaining *the mechanism of this involuntary action and by factors that work mechanically.* He attacks those who would explain the action by other means; above all he objects to the conception of tropisms—and especially of reflexes—as *originally individual actions which have shown themselves to be useful and in the course of time through habit and inheritance have become mechanical and involuntary.*

For a thorough understanding of the following criticism this view of Loeb's must be kept clearly in mind.

OUTLINE OF THE ARGUMENTS AGAINST THE TROPISM THEORY

To refute the tropism theory three lines of argument will be advanced:

1. We shall first show that the theory cannot explain all tropisms, for two reasons, (a) in many cases the necessary condition premised by the theory—namely, energy rays—may be absent, and yet actual tropisms occur; (b) in other cases, al-

though the necessary conditions are present, the tropisms occur in a way that openly contradicts the theory.

2. In the second place, it will be shown that even in cases which are apparently in agreement with the theory, the theory cannot furnish an adequate explanation of the tropisms.

3. Finally we shall set forth certain arguments which must be brought against the theory on biological grounds.

The examples that are used in the following arguments deal exclusively with heliotropism and geotropism, for to these belong the most numerous and the most exact phenomena of the whole subject. Whether chemotropism and especially thermotropism belong at all in this category is doubtful, in my opinion; galvanotropism certainly is a pure laboratory product, which for the biologist is of no interest, in so far as he wishes to study the animal, and not merely the chemical properties of protoplasm.

CASES OF TRUE TROPISMS IN WHICH THE CONDITIONS PREMISED BY THE THEORY ARE ABSENT

Tropisms without rays of energy.—I repeat again that by tropism is understood an involuntary movement definitely directed with respect to a source of energy. Such a phenomenon, notably, is the geotropism of certain aquatic invertebrates. It is either positive, making the animal creep perpendicularly downward, or it causes a horizontal movement, (diatropism) at right angles to the axis of gravity, the result of which for the organism is the so-called maintenance of equilibrium. In the majority of these cases, and to these we shall confine ourselves, the geotropism is bound up with definite sense organs, the so-called *statocysts*, with whose structure I shall assume the reader to be acquainted. It has been shown that their function depends directly upon the fact that the heavy statolith exerts a mechanical stimulus upon the sensory epithelium of the statocyst. The whole action of the apparatus, which is to bring the animal into a definite position with respect to gravity, then takes place because this mechanical stimulus acts in a direction determined by gravity, in consequence of the moveability of the statolith, which always seeks the lowest point in the wall of the statocyst cup. The theory of statolith pressure is demonstrated by Kreidl's famous experiments with iron statoliths in crustacea, by which he showed with a magnet that the movements of the

animal differ according to the direction from which the attracting force comes. Prentiss[5] and I[6] have further shown that the loss of the statoliths alone has the same effect as the loss of the whole organ.[7]

There is here absolutely no such *action of energy on the living tissue* as the tropism theory requires; the energy acts upon the lifeless statoliths, and the whole phenomenon belongs in the category of mechanical stimuli, and consequently is excluded from Loeb's scheme.

Other phenomena that are often cited as tropic movements that take place without the conditions assumed as necessary by Loeb, but which are normal in other respects, are the clearly defined avoiding reactions which infusoria exhibit toward harmful stimuli. When a number of these animals, for example, *Paramoecium* or *Stylonych a*, are placed under a cover glass the phenomena of chemo- and thermotropism may be readily studied, as many textbooks state, and in green species heliotropism is often manifested.

But since these animals are entirely asymmetrical in structure, the tropism theory is not applicable to them, because it presupposes two symmetrical body halves or a radial plan; so that these may be cited as further examples in which tropisms occur without fulfilment of the required conditions. The method, however, by which the infusoria avoid the harmful stimuli is not a swimming in a straight line away from the source of energy, but the making of so-called *trial movements*. These are, therefore, not true tropisms, as I would emphasize in agreement with Loeb against Jennings, so that these cases, like most trial movements, cannot well be used in criticism of Loeb's theory.

[5] Prentiss, C. W. The otocyst of decapod crustacea. *Bull. Mus. Comp. Zool.*, Harvard, Vol. 36, 1901.

[6] v. Buddenbrock, W. Ueber die Orientierung der Krebse im Raum. *Zool. Jahrb., Abt. f. allg. Zool. u. Physiol.*, Bd. 34, 1914.

[7] According to E. P. Lyon the case is different in certain fishes, since here, when the statoliths are carefully removed without injuring the sensory epithelium, no resultant loss of function is observed. The accuracy of this observation seems doubtful to me, because blood clots, which are almost unavoidable in the statocyst cup, apparently may assume the rôle of the statoliths. For our present discussion, however, the fish behavior is immaterial, since we have only to show in this case that *certain* geotropisms, not all, belong in the category of mechanical stimuli.

CASES IN WHICH THE PREMISED CONDITIONS OF SYMMETRY AND OF ENERGY RADIATION ARE PRESENT, BUT THE MOVEMENT TAKES PLACE IN A WAY THAT IS CONTRARY TO THE TROPISM THEORY

Sidewise movement of crabs. — Three examples only will be cited of tropisms that take place in a manner that is contrary to the theory. The clearest of these, already discussed by H. S. Jennings, is the sidewise movement of crabs. The facts may be stated in a few words: If a crab is stimulated in any way, for example, by a strong light and from one side only, there is *no* turning of the animal until its axis of symmetry coincides with the ray of light, as the tropism theory requires, but at once the crab moves sideways away from the light. This cannot be explained at all by Loeb's theory; it shows, rather, in the clearest way that the light does not act separately upon the two body halves, but upon the body as a whole, and, in consequence, a harmonious activity of all organs of movement is the result. Loeb, indeed, makes some objections to this criticism. He writes: "I am rather inclined to draw another conclusion, namely, that in the first place, in crabs an entirely different relation exists between the retina and the locomotor muscles than in other crustacea and in most animals; and that in the second place an especial peculiarity exists in regard to the function of the two retinas, in that these do not behave as symmetrical superficial elements. There is here, in my opinion, a new discovery to be made." (1909, pp. 48-49.)

It will be seen later why Loeb suddenly calls to his aid the special structure that he has hitherto neglected, but it would be difficult to say that his reply has in any way weakened the evidence against the theory. In this case an error has certainly crept into Loeb's reasoning. His explanation means, in somewhat plainer words, that in the crab in supposed opposition to other crustacea the eye is not only related with the legs of one side, which causes a turning of the animal, but with the legs of both sides, which results in another kind of movement. The real meaning of the tropism theory is not, however, that light may cause any *desired* movement, but that it does cause a *definite* movement, namely, that which leads the animal away from the light; and, as Loeb himself has emphasized again and again, this is only possible, in accordance with his theory, when

the movement in a straight line toward or away from the light involves a *symmetrical muscular movement of both symmetrical body halves.* Now the sidewise movement of the crab, although it is a movement in a straight line away from the light, is caused by an *asymmetrical cooperation of both sides,* since, for example, in moving to the right, the legs of the left side push the body so that the extensors are in activity, while the legs of the right side move with the flexors doing the work. This is not explicable by the theory and can only be understood as a purposeful and elaborate corporate action of the animal. The disagreement with the theory could scarcely be greater. The assumption is also untenable that the action of energy upon a symmetrical form is here concealed by some hypothetical second factor. For since the light, if the action takes place according to Loeb's scheme, must cause a turning of the crab, then this second factor, which inhibits the turning, must, when left to itself, cause a turning toward the opposite side. This would mean then that the crab, when not stimulated by light, would move continually in a circle, an evident absurdity.

A second example of a tropism which occurs in a manner that contradicts the theory, in spite of the presence of all the premised conditions, is a peculiar phenomenon which may be observed in the starfish, and in a crustacean, and which I may call *changeable heliotropism.*

If a starfish is brought into a uniformly lighted field in which is a spot of light of different intensity, such as a deep shadow or a brighter light, *in both cases* the animal creeps toward this spot.[8]

Among the crustacea I have observed an analogous phenomenon in *Hemimysis lamornae.* This animal swims constantly back and forth in the aquarium, as far as the space permits, but always in a perfectly definite direction, forward toward the light coming from the window, backward away from it. This crustacean therefore changes the character of its heliotropism with each turn that it makes at the glass wall of the aquarium.

That one and the same animal should show both positive and negative heliotropism is in itself nothing remarkable and in nowise contradicts the theory, it is moreover of frequent occurrence.

[8] Plessner, H. Untersuchungen über die Physiologie der Seesterne. *Zool. Jahrb., Abt. f. allg. Zool.,* 33, 1913.

The changing of one kind of movement into another, however, is always correlated with the application of some new stimulus,[9] by means of which the physiological condition of the animal is so changed that the same optical stimulus now produces the opposite reaction. A good and clear example of this is furnished by certain other Mysidae (see footnote 12) which become positively heliotropic after lighting, negatively heliotropic after shading the field. But the change of movement observed in *Hemimysis* takes place *without* any alteration in the physiological stimulation, and in the starfish we see even that one and the same animal may be brought to either a positive or a negative reaction, according to the desire of the experimenter.

Now, according to Loeb's theory, we see in an animal a definite system of chemo-physical forces. When energy of definite constant amount acts upon such a system, the reaction must necessarily be certain and definite, i.e., with similar stimuli and similar physiological conditions in the animal, the movement must always occur in the same way. The case of *Hemimysis* is therefore not to be explained by the tropism theory.

Conversely: If two separate and distinct amounts of energy each compel a definite system of forces to make the same movement, by logic these two amounts of energy should be equally great.

This principle is overthrown by the case of the starfish, which, in the same physiological condition, is attracted by light as well as by shadow. It therefore follows that, either the starfish is not such a system of forces as Loeb assumes, or that the energy acts on the eye in an entirely different manner. What the meaning of the phenomenon is does not concern us here, we are content with the assertion that the cases of changeable heliotropism cannot be explained by the tropism theory.

The impossibility of explaining the turning around the horizontal cross axis. The turning around a horizontal cross axis is a phenomenon which nearly all Metazoa exhibit in their *heliotropic* and *geotropic* movements, and it will be recognized as a third example of tropisms which take place in a manner

[9] This need not always be an external stimulus. It is also conceivable that in the course of individual development the physiological condition may be altered by the internal changes that are going on. The behavior of many larvae which, without outward cause, change their heliotropism after a certain age, serves as an example.

entirely contradictory to the theory, although all the necessary conditions of the theory are present. Beginning with the *diaheliotropic* movements of crustacea, it should be noted that many species, marine as well as fresh water forms, always swim with their backs turned toward the light (the "light-dorsal reflex"). They move, therefore, at right angles to the rays of light, a true diatropism. By arranging the lights so that the aquarium can be lighted either from above or from below, a sudden illumination from beneath causes the animal, which has been swimming dorsal side up, to turn over on its back, so that the dorsal surface, now down, is still turned toward the light. This, however, need not contradict the tropism theory, for the elongated crustacea always turn over on their backs by turning around the longitudinal axis which lies in the plane of symmetry. Now, if we assume for the sake of simplicity that the original position[10] is somewhat oblique, the theoretical scheme may be applied as follows: Unlike illumination of the two symmetrical body halves results in a turning of the organism until it reaches the final position, symmetrical with the rays of energy. The short-bodied compressed crustacea, however, behave in a very different manner on account of their structure, turning over on their backs by turning a somersault. The amphipod *Hyperia* always does this, the larvae of *Squilla* very often, and these are only two examples of a very frequent occurrence. Such a somersault utterly disregards all the preconceived rules of the tropism theory in that there is no turning of the body around an axis in the plane of symmetry. There is instead, a turning around a horizontal cross axis *perpendicular* to the plane of symmetry, through which no plane can be passed dividing the body into two symmetrical halves, as the theory requires. It is therefore utterly impossible to bring this movement into harmony with the theory, and yet it is a genuine tropism.

Exactly the same consideration applies to the *diageotropic* movements of those crustacea which swim ventral side up, manifesting the maintenance of equilibrium instead of the "light-dorsal" reflex. The crustacean *Palaemon* may be chosen

[10] The reversed symmetrical position, in this case with the plane of symmetry in the direction of the light rays, but with back turned away from the light, presents great difficulties for an explanation by the tropism theory (see p. 352).

as an example. As soon as this animal is removed from its normal horizontal position, with ventral side up, involuntary movements restore the original position. This kind of orienting movement can be reconciled with the tropism theory only when a turning around the long axis occurs. But place the *Palaemon* nearly perpendicular to the surface, and it will recover its normal position by turning around the horizontal cross axis, which, as we saw above, prevents any explanation by Loeb's theory.[11]

These diatropic movements cannot be ignored. They represent typical movements of orientation with reference to a source of energy, and are thoroughly genuine tropisms. Loeb must accustom himself to the idea that, in addition to the sidewise movements of crabs, there is another great category of phenomena which do not agree with his theory.

Without dwelling longer on the examples of diatropic phenomena, which after all, are relatively infrequent, let us consider any organism with positive or negative heliotropism which moves freely in space, perhaps swims. When the source of light is really on one side of it, the animal will conform entirely with the scheme of the theory by turning around a vertical axis which lies in the plane of symmetry, but if the light is either above or below it, then the animal will turn, as any experiment will show, around the cross axis, which is, as we know, contradictory to the theoretical expectations.

We see here once more what the observation of *Squilla* and *Palaemon* has already shown us, that in one and the same animal certain tropisms occur which *seem* to be explained by the theory, together with others which are seen at the first glance to be entirely inexplicable. Surely no one would wish to separate these two movements, the turning around the *vertical*, and the turning around the *horizontal* axis, or to assert that although the first is conditioned by the general laws of the tropism theory, the second requires a very different kind of explanation, namely that of the specific structure of the animal. No! Both movements, which frequently replace each other and can be combined in various ways, are *fundamentally alike*. Since it can

[11] *Palaemon* reacts also after loss of the statocysts, as I have shown, by means of the general position-reflex, which, since we know little about it in detail, may itself be open to explanation by the tropism theory.

be shown that one of these movements has nothing to do with the tropism theory, we shall come to the conclusion that the other, the turning around the vertical axis, is also only *apparently* connected with the tropism theory, but in reality is caused by the purposeful adaptive structure of the organism.

THE IMPOSSIBILITY OF EXPLAINING THE REACTION WHICH RESULTS FROM THE REVERSED SYMMETRICAL POSITION

In the above section we found for the first time an argument that is applicable to all tropisms. The turning around the horizontal axis furnished convincing evidence entirely contradictory to Loeb's theory, but it is different with respect to the turning around the vertical axis. In case that the evidence against the tropism theory already presented should be considered insufficient upon this point, (resting as it does, so far as this point is concerned, on reasoning from an analogy) we will now especially examine these movements, which were apparently the only ones Loeb had in mind. We shall show that even for these movements (of turning round the vertical axis) Loeb's assumption leads to consequences which contradict the facts; this will be shown first for a particular case,—that of the reversed symmetrical position.

If I take any bilaterally symmetrical negatively heliotropic organism and place it as exactly as possible so that the anterior end is turned to the light, the facts of the experiment are as follows: The animal turns itself very quickly through 180°, and swims, flies, or creeps away from the light. Now I ask you to consider that the whole principle of the tropism theory is founded upon the dissimilar action of energy upon both symmetrical body halves. In the present case there is no such dissimilar action, since both sides of the animal are stimulated by the light in exactly the same degree. In consequence, if the relations were actually what the tropism theory assumed, then a reaction would be either entirely lacking, or else would take place very gradually, after the animal had lost its symmetrical position through accidental, small movements. In other words: According to the tropism theory, the position with head turned away from the light for positively heliotropic animals, and that with head turned toward it for negative forms, must be a so-called "dead center" or point of no motion. An indisputable

line of thought, not to be answered by argument, mutatis mutandis to be applied to every kind of tropism.

That a quick and precise reaction always takes place even in the reversed symmetrical position, as every experiment proves, can be only explained by the fact that the organism as a *whole* is sensitive to the unusual position and reacts to it. On no account can the reaction be explained by the opposed actions of the two body halves, for such actions would mutually destroy each other. This is the most generally valid argument that can be brought against the tropism theory and it applies to all existing tropisms. The reaction which always may be observed with the reversed symmetrical position cannot be explained by any reflex mechanism, at least, very complicated hypothetical assumptions would have to be made; it shows clearly that even in the lower animals there are voluntary actions which take place as a result of unpleasant sensations, or whatever one may please to call them.

THE IMPOSSIBILITY OF EXPLAINING THE HARMONIOUS COORDINATION OF THE MOVEMENT OF THE TWO BODY HALVES

The argument just presented, that the reaction of the animal does not depend upon the independent action of the two body halves but represents a harmonious working together of the whole organism, applies, not only to the reversed symmetrical position, but especially to almost every tropic turning around the vertical axis. If such a movement took place in accordance with the scheme of the tropism theory, it might be compared with a row boat containing two men, one pulling the right oar, one the left. If one pulls better or harder than the other, the involuntary result is that the boat begins to turn. Both sides act without coordination and the turning is caused by the *difference* of the opposing forces of the two sides. This case corresponds exactly with the tropism theory, and is exemplified even to the minutest detail in *galvanotropism*.

But there is another possibility for turning the row boat. Should the oarsmen *intend* to turn around, then one of them must row harder than before, while the other will either reverse his stroke to help his partner, or row gently so as not to hinder him. This result is also a turning, but it is caused by the *coordinated purposeful* working together of the two sides; in the

first case by the *sum* of both forces which work in the same direction, in the second case by the force of one side alone. *The criterion is that there is no opposed action of the two sides.* This case is exemplified in all tropisms which occur in nature and it evidently cannot be reconciled with Loeb's theory. Some examples will now be mentioned.

The first concerns the diaheliotropic movements of marine crustacea, the "light-dorsal" reflex which has already been described. Two years ago I showed that illumination from one side always produces a sidewise paddling of the swimmerets of *both sides with the same tendency*, a clearly coordinated and purposeful action which it is impossible to explain, or even to obtain, according to the tropism theory. Such an interaction of the musculature of the appendages of both sides may be observed in the entire animal kingdom in almost all movements involving a facing about. Until recently, however, very little interest has been shown in these matters, which are of great theoretical importance.

The second case, in which one side of the body moves while the other remains perfectly still, is naturally rarer. The best known example is the behavior of the Mysidae in response to light stimuli, studied by Bauer[12]. These peculiar animals are positively heliotropic after having been exposed to light, but are negatively heliotropic after shading; in the first case therefore, darkening, in the second case, illumination, is the stimulus that makes the animal try to escape. The escape takes place through the fact that the legs turned away from the stimulus have their movements inhibited, while those turned toward it keep on paddling, so that necessarily a turning away from the place of the stimulus results.

So much for the facts. If we try to find their meaning, it is clear, first, that the result is not unfavorable for Loeb, since *de facto* only those legs react which are connected with the stimulated eye, and therefore the movement *can* be regarded as not coordinated. On the other hand, it must be admitted that the movement, like that of the row boat, can just as well be regarded as a purposeful and coordinated one, since there is no hindering of one side by the other. We find ourselves to some extent on

[12] Bauer, V. Ueber die reflectorische Regulierung der Schwimmbewegungen bei der Mysideen, etc. *Zeitschr. f. allg. Physiol.*, Bd. 8, 1908.

neutral ground in regard to this interesting question. We cannot prove that the phototropism of the Mysidae is evidence against the theory, but neither can Loeb show that it is evidence in his favor.

THE IMPOSSIBILITY OF FINDING THE AXIS OF TURNING

The three last-mentioned arguments against the tropism theory have been unaccountably overlooked by most critics until the present time. The same is true of a fourth which will be considered next.

Any bilaterally symmetrical organism that is sensitive to light will serve as an example, but to select one of Loeb's own, let us take the winged aphid. If this insect is illuminated from the left side only, (meaning that the source of light is neither above nor below, but exactly on a level with it), it will turn immediately and fly in a straight line to the source of light. This is a very clear case of heliotropism, in Loeb's sense. Illumination of one side, result: unequal movement of the two sides until a position is reached which is symmetrical with respect to the source of light; finally, flight in a straight line to the light.

Now how much of this can the tropism theory explain? Evidently, setting aside some considerations to be discussed later, only the point that the two sides of the body move differently. Now from this, logically, a turning of the whole organism around *some* axis lying in the plane of symmetry, xy, must result, which turning continues until the plane of symmetry coincides with the plane xyL (L = point of light). But that is all that can be obtained from the tropism theory! The theory does not reveal around which one of the innumerable axes of this plane a turning takes place. And yet, in order to reach the source of energy, the turning must be around a *definite* axis, namely, one perpendicular to the line joining the organism with the source of energy. Any theory which deals earnestly with the present problem should explain how the turning takes place around just this one axis, or in other words, how the movement can occur in a few definite flight-muscles out of a great number. Were Loeb's theory our only resort it would be necessary to assume a miracle to understand how the aphid ever gets to the light. If point A is the animal, point L the light, and if I assume that the turning required by the theory is ended, and

therefore the line AL lies in the plane of symmetry of the animal, the animal can then assume different positions according to the axis around which it has turned. Consequently, without disregarding the conditions of the theory, it can move, according to the direction of its long axis, along any line running from A out into the plane of the paper, only one of which, AL, leads to the light. There could be no clearer demonstration of the inability of the tropism theory to furnish an explanation which is clearly its function to give. That a direct movement toward the light actually takes place is not to be explained by such physico-chemical assumptions as Loeb makes, it shows rather, that in the interior of the organism is a *purposefully functioning mechanism*, which, in response to the light stimulus, sets the locomotor organs into such activity that a general movement toward the light must follow. The morphological-physiological structure of the animal is consequently responsible for the occurrence of the tropism, and this structure must be investigated in every separate case.

THE DISAGREEMENT OF THE TROPISM THEORY WITH THE PRESENCE OF A REFLEX ARC

The question now arises of the relation of the tropism theory to the special structure of the animal, or in other terms: if it can be shown that the stimulus from the eye traverses a definite path, a so-called reflex arc, how does the tropism theory apply to this fact?

The unprejudiced observer will certainly be inclined to consider that the cause of the tropism is this reflex arc, which somewhat resembles the works of a clock where one wheel clutches another until the hands move, and that any farther explanation of this phenomenon is superfluous.

On the other hand, in looking through Loeb's writings, we are astonished to find that his opinion is quite different. This is most clearly shown in the case of the crab's sidewise movement, the facts of which we have already considered. Jennings having previously made the criticism that the behavior of this animal could not be harmonized with the theory, Loeb replied in the following words, which have already been quoted on p. 347: "I am rather inclined to draw another conclusion, namely, that in the first place, in crabs an entirely different relation exist

between the retina and the locomotor muscles than in other crustacea and in most animals; and that in the second place an especial peculiarity exists in regard to the function of the two retinas, in that these do not behave as symmetrical superficial elements."

He therefore not only does not deny the existence of the reflex arc, but uses it to explain the existence of the phenomenon, and yet he still stands by the tropism theory *in toto*. The solution for this enigma has escaped his recent critics; it will only be discovered by recalling the historical development of the tropism theory which may be told as follows: The phenomenon which shows the peculiarities of tropic movements in the clearest and sharpest manner is undoubtedly *galvanotropism;* the theoretical estimate of the remaining tropisms was then made by analogies drawn from this first phenomenon. Now the relations in galvanotropism are of a very special character. It does not occur in nature and is a pure laboratory product. So far as it is concerned, the animal is no machine with the definite tasks of the maintenance of its own life and the propagation of the species, but is solely a *symmetrical form the two sides of which possess a similar chemo-physical structure*. Expressions like adaptation and function are not needed here, and if a future chemist should ever succeed in producing from inorganic matter an animal like Faust's homunculus, this being would have no relation to function, natural selection, adaptation, etc., but would infallibly manifest the phenomena of galvanotropism. The organism in this case might be compared with a crystal, which does in fact possess a structure, from which on the application of certain energies definite resultant phenomena are manifested, but to which the conception of adaptation would be wholly inapplicable.

The fundamental mistake which Loeb and his followers make is to apply indiscriminately what they find true for galvanotropism to all tropisms that occur in nature. The idea of adaptation is here no empty delusion. If Leob actually denied the statement that *the animal is a machine adapted for self-maintenance and for the propagation of the species*, then no further discussion would be possible, but for his own sake, and for the sake of his reputation as an investigator of nature, I assume that he does not go so far. If, however, he is prepared to admit

the above statement, then in return we can assure him that we regard the actions of lower animals just as he does, as involuntary, and that for the most part we reject any idea of free will; he must then discuss certain questions with us.

For example: The eye of the heliotropic *Balanus* larva is of little use in enjoying the beauty of the surrounding scenery; we assert this because we, like Loeb, deny the larva's higher intelligence and free will. In consequence, we are forced to the view that the purpose of the eye, for it must have some purpose, is to enable the heliotropic reflex to take place, at least we know of nothing else for which the eye might serve. It therefore follows that the entire reflex arc, which alone it is that makes the eye capable of functioning, is purposeful. In going so far we finally cannot escape the view that the cause of the tropism is just this mechanism of the reflex arc, so adaptive in construction and in function, and that energy plays no other rôle than to set the apparatus in motion.

If Loeb replies to this deduction that all tropisms must then have a biological use, the following is my answer: The contrary assertion is in no way proved; if in many cases the tropism seems useless or even harmful for the animal, it is highly probable that we either do not understand what its use is, for we know painfully little of the normal needs of the lower animals,[13] or it may be, that during the experiment the experimenter has kept the animal under unnatural conditions, a case that is only too frequent.

To condense and recapitulate the foregoing argument: The facts are, that light, with the help of the eye and the associated reflex arc, starts a definite movement, of which light is one condition, the reflex arc the other condition of its occurrence. No conclusion can be reached from this statement, either for or against the tropism theory. The latter theory acquires meaning only when to the facts we add a definite definition of the expression "animal," defining it simply as a form with definite chemo-physical structure, without any reference to the purposeful nature of its structure. Upon this form, then, the blind natural orce acts ust as iron upon a magnetic needle, and so

[13] A more detailed consideration of this point would carry us too far. I will, however, call attention to the valuable work of Franz, "Die phototaktischen Erscheinungen im Tierreiche und ihre Rolle im Freileben der Tiere," *Zool. Jahrb., Abt. f. allg. Zool.*, Bd. 33, 1914.

we get a tropism. This definition of an animal, however, is false, and, in consequence, so are the conclusions that are drawn from it.

The animal is rather a mechanism of purposeful adaptive construction for the tasks of self-maintenance and reproduction. This is an unassailable truth; therefore it follows that the separate organs, for example, the eye, have a definite purpose, as the adaptive structure of the eye well shows, and even though this eye causes nothing but a heliotropic movement, in the last analysis, the reflex arc which enables the movement to take place must be considered as a purposefully constructed mechanism. Therefore this very mechanism is the cause of the tropism and the tropism theory is entirely superfluous. This argument refutes the tropism theory so far as those lower animals are concerned whose eyes are only heliotropic in function.

One exception must be made. In highly developed sense organs the matter is somewhat more complicated. If, for example, an eye is adapted for perceiving images as well as for allowing heliotropic movements, one might assume that here *image perception alone is the purpose of the eye*, while heliotropism is but one of nature's unintended by-products.

In this case, one might almost assent to Loeb's view, were it not for those arguments already known to us which are based upon the details of the movement, and which entirely refute the theory. The existence of a reflex arc makes the theory superfluous, at least in many cases, and robs it of any content. Tropism then finds its cause in the *reflex arc* itself. It can neither be "explained" away nor denied, it is a simple fact of observation which leaves no room for a theory.

In all further cases, where such a reflex arc is not clearly demonstrable, but a nervous system exists which connects muscles and sensory epithelium, it is most probable that only our lack of operative skill prevents us from finding the reflex arc, and that it is perhaps never absent. This again lessens the theory's right to exist. I should like to bring such a case under closer consideration because it demonstrates so clearly the entirely unproved assumptions upon which the supporters of the tropism theory depend. Davenport (1897) writes in regard to the negative heliotropism of the earthworm: "*The sun's rays may fall horizontal and at right angles to its axis. Then the rays strike it* (*the earthworm*) *laterally or in other words, it*

is lighted from one side and not from the other. Since now the protoplasm of both sides is adapted to an equal amount of light, the side that is least lighted is nearer to the optimum strength of light. Its protoplasm is in a phototonic condition, while the strongly lighted side has lost its phototonic condition. Therefore the darkened muscles are in a condition to contract normally, and the brightly lighted ones are relaxed. *Under these conditions the animal turns toward the darker side.* * * *" "Dichtung und Wahrheit,"—poetry and truth—might be placed as a title above this entire statement. Truth is found only in the italicized[14] first and last sentences. What lies between can only be admired as evidence of a richly endowed imagination, it has no scientific value. We know nothing about what strength of light the "protoplasm" is adapted to. Its phototonic condition is completely hidden from us and consequently also the action of light upon darkened and lighted muscles. What we really know is that in and beneath the epithelium of the earthworm cells are found whose structure certainly indicates that they are sensitive to light, that from them nerves run to the ventral nerve cord, and other nerves from there to the muscle-layer of the skin, further, that the whole tropism ceases if I destroy the ventral nerve cord, so that we may suspect the existence of a reflex arc: epithelial cells sensitive to light, sensory nerves, ventral nerve cord, motor nerves, and muscle layer. Without hesitation I leave it to the reader to decide which of the two possibilities, the reflex arc or Davenport's assumption, is more probable. A certain possibility remains for an explanation in Loeb's sense. Assuming that the criticisms made above are unfounded, and referring exclusively to those cases where no reflex arc is at present demonstrable, then, from this standpoint, the tropism theory is master of the situation.

I wish here to draw attention to two tropisms of this kind (with no demonstrable reflex arc). The *first* concerns the reactions to the stimuli of gravity of such animals as are known to have no statocysts, especially those which still manifest geotropism even after the removal of these organs. The *second* concerns the growth phenomena of certain hydroid polyps which result in placing the animal in the direction of the rays of light.

[14] The italics and the words (the earthworm) are the present author's.

In both cases we are entirely unable to analyze the phenomenon if we wish to rest on a basis of *fact*. Nothing is more characteristic of the tropism theory than the fact that it flourishes best in these darkest corners of our knowledge. It is far easier to construct a theory in regard to things of which one knows practically nothing than about things which have been studied thoroughly, for then the theory is in continual danger of being impaled upon the rough edges of facts. These two tropisms would be insufficient to impale the theory were it not for the other arguments which are available as evidence in this case.

THE IMPOSSIBILITY OF EXPLAINING THE PURPOSEFUL NATURE OF TROPISMS

After having considered the arguments against the tropism theory from the morphological side, we shall now take up an argument from the biological side, namely, the purposeful nature of tropisms. It is usual to try to solve the problem of such movements as are seen in tropisms, by considering the structure of the animal as a *given premise*, and by limiting one's self to the movement as determined by certain elements of this structure and by definite external stimuli. The purposeful nature of the movement for the whole organism is then seen as a consequence of the structure. Purposefulness is therefore, wherever demonstrable, also a mere fact of observation, about whose origin we need not trouble further.

Loeb, however, takes an opposite view. For him, the structure of the organism is a negligible quantity which he quite overlooks in reaching after the higher spheres of physical chemistry, the universal panacea of modern investigation. The corner stones of the tropism theory are merely the symmetry of the animal and blind unorganized natural force, e.g., light. If from the interaction of these two factors a truly purposeful action results, it is most astonishing and some explanation is absolutely demanded from Loeb. His only possible means of escape is the selection theory, toward which, by the way, he takes a very peculiar and extraordinary position.

On one hand he denies any value to selection and writes: "Whoever does not want to waste his time in an idle play of words will do well to analyze instinct in the same manner as is done for occurrences in the inorganic realm, where expres-

sions like adaptation and natural selection are demonstrably useless and where the only concern is to make clear the mechanism of the occurrence," (1913, p. 452). I find, however, another place where he openly states: "that species manifesting tropisms which would be incompatible with the reproduction or maintenance of their kind must die out," which is in principle an affirmation of the idea of selection.

Whatever Loeb's position toward Darwin may be, it is certain, whether he admits it or not, that he needs Darwin as an ally, if he intends to explain the purposeful nature of tropisms.

It is all the same to us whether harmful tropisms, the existence of which we can rightfully contest, occur together with indifferent and useful ones, if only the origin of the useful tropisms can be established.

Some examples will now be given of tropisms which serve some purpose for the whole organism.

There are many animals in which the tropism takes the form of a movement of flight to avoid an enemy's attack. Certain species of *Cypris* living in open water are rendered positively geotropic and negatively heliotropic by mechanical disturbances; that is, they seek the deepest and darkest part of the water. On the other hand there are inhabitants of dark localities, which, when disturbed, respond with positive heliotropism, thereby avoiding an animal which is burrowing in the mud.

In other cases the tropism of food getting may be seen. Loeb himself gives as an example the behavior of the young caterpillar of *Porthesia*, which, creeping out of its winter nest can only find the young leaves at the tip with the aid of positive heliotropism.

One case should be mentioned where movements of this kind occur in response to need of air, for example, the water scorpion, *Nepa*, after using up its air becomes negatively geotropic and positively heliotropic,[15] and it thus rises to the surface of the water where it can get a new supply of air. In the same category probably is the positive heliotropism of the Daphnids, described by Loeb, which they manifest when certain acids, especially carbonic acid, are added to the water. This tropism evidently aids the animal in seeking fresher water levels.

[15] Baunacke, W. Statische Sinnesorgane bei den Nepiden. *Morphol. Jahrb., Abt. Anat.*, 1912, Bd. 34.

Finally, there are many cases in which positive heliotropism forces great masses of young larvae to make purposeful movements which scatter them abroad in the water. There are many more examples and they will certainly increase in the future as our knowledge of the mode of life of the lower animals becomes more profound.

How can Loeb, if he stands by the tropism theory, explain the evidently purposeful nature of these tropisms?

The exact course of action in such movements must be considered if one is really to understand them. In the case of the *Porthesia* caterpillar hunger is the conditio sine qua non for the occurrence of the tropism, and this, in its turn, leads the caterpillar to the nourishing leaves. We have here a physiologically harmful condition, which of necessity causes a movement which ends the harm. Hunger is therefore to some extent its own physician!

Few words are required to show that this is evidently not a simple but a very complicated occurrence. If we wish to explain its origin with the help of the selection theory then it must be assumed that an elimination of unfit individuals takes place in two ways. On the one hand, all those caterpillars must perish which do not move directly toward the light but which move in a diaheliotropic manner, and of the selected individuals all must die which manifest the tropism under other circumstances than those of hunger. For should the impulse remain after the twigs are stripped bare death must surely follow.

In both these cases the survivors would be only a small minority, and with such a decimation it would be astonishing if there were any *Porthesias* left.

Discussions of the selection theory never lead to an entirely certain conclusion, but always to probabilities. I believe I have shown that in our case the possibility of an explanation by selection is very slight. It will naturally be even slighter if we consider combined tropisms like those of the water scorpion and the *Cypris*. Loeb has not concerned himself in any detail with the problem of the purposeful nature of tropisms. But it is not without amusement that we note that he, who regarded the consideration of the question of selection as " a loss of time in an idle play of words," should be forced to an ultradarwinian conclusion by a logical analysis of his own theory.

SUMMARY AND CONCLUSIONS

The tropism theory is not applicable to all tropisms for the following reasons:

1. In many cases the conditions premised by the theory are absent, and yet true tropisms, that is, involuntary movements regulated by a source of energy, take place. Example: The *action of energy* in geotropism *is lacking* in so far as it is connected with the presence of statocysts. The movement is the result of a mechanical stimulus caused by the statoliths.

2. In many cases, although the conditions premised by the theory are present, the tropisms take place in a manner that contradicts the theory. Examples: (a) Sidewise movement of crabs; (b) changeable heliotropism of certain marine animals; (c) turning around the horizontal cross axis not in the plane of symmetry, to be observed in all tropic movements.

There remain now, as possibly to be explained by the theory, only those cases in which *symmetrical animals manifest a turning around the vertical axis*. But here also the theory is unsatisfactory, because:

3. The theory cannot explain the reaction which results from the position of reversed symmetry.

4. The theory cannot explain the coordinated working together of the two sides of the body.

5. The theory cannot tell why the turning always takes place around the axis which is perpendicular to the line joining animal and source of energy; in other words, it especially cannot explain how the animal finds its way to the source of energy.

6. The presence of a reflex arc in many cases renders the theory entirely superfluous and without meaning, for the movement is already satisfactorily explained by the reflex arc itself.

7. The theory cannot explain satisfactorily the undeniably purposeful nature of many tropisms.

On the other hand, one positive result of our investigation is that wherever tropisms occur a purposeful adaptive mechanism for movement is found which has the task of guiding the animal to the source of energy, and that during the movement the organism always acts as a whole. We shall therefore adhere to our old opinion that tropisms, like all other reflexes, were originally individual actions, which, in the course of time, have become mechanical and involuntary. This view will not con-

tent everybody, for it requires the acceptance of certain unproved assumptions, but at least it is not contrary to facts.

It seems to me of the utmost importance that tropisms should not be taken out of the class of other reflexes. If we observe the reactions of the animal to light, from the simplest sensory reflex up to image perception there is a continuous chain of increasingly complex reflexes, whose common attribute is that with the light stimulus definite muscles become active. Physiologically, therefore, these movements are all alike; it is consequently inadmissable to explain some of them in a way that contradicts what is true of all the others.

It is hoped that the arguments here brought together will be sufficient to make the tropism theory disappear from zoological literature.

The theory is useful only in so far as it shows that the application of the inorganic sciences to the problems of biology is of very limited range. I do not wish to be misunderstood upon this point. There are certain problems, and many of them of great importance, which can only be solved with the aid of chemistry and physics. But such problems always concern merely the study of *single organs*, perhaps of muscle, which is evidently a chemical energy-machine, or of the alimentary tract, which represents a chemical manufactory. Here and in a thousand analogous cases, with which naturally the physiology of the senses belongs, the physical chemist finds a rich field of activity. Just as soon, however, as we observe many organs working together, whether in a system of organs or in a whole organism, we are confronted everywhere, in the morphological structure as well as in all physiological processes, or the so-called " psychic " actions of the animal, by *adaptations of purposeful nature*. Whoever denies this, only shows that he is insufficiently acquainted with facts. Purposeful structures, however, cannot be explained by physical chemistry. The chief fault of Loeb and his followers is that they have overlooked this point.

We have found it universally true that in all tropisms the fundamental mechanism of movement is adaptively constructed, for the purpose of leading the animal toward or away from the source of energy. Loeb's attempt to refer the actions of the lower animals to chemo-physical processes should therefore be

disregarded for the future. The trend of his investigations is not only unfruitful in itself, but it leads to a shallow rather than to a deeper conception of the whole of biology, since it inclines to regard the whole problem as solved just as soon as the chemo-physical side of it is explained.

The statement, for example, that the spermatozoa of the fern are attracted by malic acid seems to those of this temper as a most satisfactory view. The " mechanism " of the occurrence is explained and one turns contentedly to other things. But what is actually gained? The problem really consists in the fact that the archegonium secretes just that substance to which the spermatozoon reacts. It is a most delicate adaptation, such as we find everywhere with closer observation, but whoever limits his view to chemo-physical processes will pass by this main problem without even seeing it. Biology is above all a historical science, it deals with things which have taken place, the investigation of which must be carried on necessarily from other points of view than the investigation of inorganic material. Physics and chemistry teach us chiefly to recognize the means which nature uses to attain any purpose in the realm of living matter, they cannot reach the deeper problems. Only when the physico-chemist is convinced of this can he work successfully within the field of biology.

NOTES

NOTES ON THE BEHAVIOR OF CERTAIN SOLITARY BEES

PHIL RAU AND NELLIE RAU

Colletes compactus[1]

The September afternoon was bright and sultry, with a temperature of perhaps 85°, as we trudged up a deep little valley between heavily wooded hills, where a tiny brook ran away from a spring. As we stepped over the stream, the hum and blurr of swarming insects attracted us. There at the side of the water was a swarm of *Colletes* bees, perhaps two hundred in number, buzzing, flying, wheeling, dancing, weaving in and out, all in a chosen spot a few inches above the pebbles at the water's edge, and in an area about two feet across. The excitement was riotous, dancing and mating, dancing and mating. The males were far in excess of the females, apparently in about the proportion of three or four males to one female. The females were not so active as the males, but sat down more often upon the rocks as if in quiet and meek anticipation of attention. And usually they rested only a few seconds before their mates arrived, often from two to five males struggling together for the possession of one female. I am not sure whether the female's deliberation was of psychological or physiological causes; matings were not seen to take place on the wing, but she was of heavier build than the male and also was frequently laden with pollen; this may have hindered her participation in the merry dance. They were so intent upon their frolic that we could pick them up easily with the forceps, and our presence scarcely disturbed them; when we stepped into the very midst of the swarm they scattered a little—of necessity—but returned and concentrated on the same spot as soon as we removed ourselves.

[1] We are indebted to Mr. J. C. Crawford for the identification of the three species herein mentioned.

We could see no reason why this spot should be more agreeable to them than any other. Some lime had been thrown over the rocks at this point, but we could not see why this should attract them, since they paid it no heed. Other lime-dumps were near by, which did not attract them.

Calliopsis nebraskensis Cfd.

Some little solitary bees, *Calliopsis nebraskensis* Cfd., often busy themselves upon a bare spot in our field. They live in holes in the ground, and while they are solitary in habit they often exist in communities, i.e., several holes occur near together, but we have not ascertained whether this is because they prefer the community life, or whether merely the desirable features of the sunny bald spot has brought them near to each other.

These holes are always found closed and covered with a little mound of loose, well-pulverized earth. Not infrequently one sees this loose soil move, but evidently the occupant of the hole is only pushing up more dirt from below. Only rarely does one see her come tumbling out through the top of the mound, gather herself together and shake off the dust all in an instant, while the loose dirt again closes behind her, and dart off on the wing. It is a wise precaution that she keeps her nest always covered, for I have seen vandals prowling about these homes more often than I have seen the rightful owners. In fact, I long thought that these burrows and mounds actually belonged to certain tiny black-and-red wasps, who make very bold in the liberties they take about them.[2]

Now these little bees have one strange antic which has aroused our curiosity a number of times. First, one's attention is attracted to some little object buzzing around on the dusty ground, in the manner of an insect which has fallen upon its back and is struggling to get on its feet. It is a pair of these little bees, clasping each other by the legs, ventral to ventral, and with their bodies curved, so that the two united form almost a ring. Thus they continue buzzing and spinning and tumbling about on the dusty ground, whirling 'round and 'round in small circles near the same spot. In its intensity the struggle has much the appearances of a miniature dog-fight. I have never been so

[2] This was later identified as the parasitic bee *Specodes sp.* by Mr. S. A. Rohwer.

fortunate as to see the beginning of one of these performances, but they have continued for thirty seconds to a minute after discovery.

At first we thought it was a mating performance, but later we found a pair in actual copulo, sitting quietly on the ground, the male surmounting the female with the abdomen curled underneath hers to effect the union. The duration of this mating was perhaps five minutes. But what the significance of this whirligig struggle may be we have not yet determined. At the conclusion of the performance they have always separated and instantly darted away with a buzz, so we have failed even to determine the sex of the performers. Is it a friendly or an antagonistic encounter, a sexual or merely social or platonic frolic? There may be some of the elements of courtship about it, but so far as we have seen it does not immediately precede or follow mating.

Megachile brevis Say.

We were plodding along the railroad track one hot, mid-July day, hunting for ground-wasps, when a little creature emerged from a crack in a tie at our feet and darted away on the wing. It was a little leaf-cutter bee, *Megachile brevis* Say. After one or two minutes we spied it returning, coming up the track from the east; it located its particular crevice without the least difficulty, entered, reappeared after a few moments and went off directly down the track to the east again. Soon she returned, coming straight along the track as before. and entered her hole without displaying the least confusion. This time she remained in for five minutes, and even a heavy train passing on the parallel track and shaking the earth perceptibly did not alarm her away.

When next she emerged she sailed directly west, with a dash. She flew with a characteristic gait, neither gliding nor zig-zag, but a combination of the two, like a boy on skates making a smooth, gliding stroke, first with one foot and then the other. She flew about twelve or fifteen inches above the ground, and kept pretty accurately to the same level. After ten minutes she reappeared, coming down the track between the rails, carrying her bit of green leaf, about one-half inch long. This time

she approached from the west (a new direction), and she betrayed extreme confusion, flying back and forth in the region of her tie and finally alighting on a weed near by to rest and readjust her burden and get a better grip upon it with her hind pairs of legs. At this point a train dashed by, passing over her very tie, shaking it violently, and causing her to disappear for seven minutes. Then we spied her up the track, hunting eagerly over another tie which had a wire over it, just like her own. Furthermore, she was searching over *only* the south end and west side of the ties (this was the location of her nest in her own tie); then she seemed to give it up and dashed off down the track to a few feet beyond her nest and resumed the searching, then gradually worked her way back, circling low over the south end of many ties until she came to her own which she recognized at once and wearily entered, carrying all the time her green leaf. After a four-minute rest she dashed off westward again, this time for a fifteen-minute journey. Upon her return she repeated exactly the performance of searching over the ties a little west, then east of her nest, and then working back to the middle position, where lay her nest. At each trip she brought her load of leaf. As she emerged from her crevice after five minutes we caught her and dug out her nest, a neat little pack of leaves about three-fourths inch long.

It seems to me that she was quick to make use of her newly-acquired knowledge that she could rely upon the rails as guide-lines to her home, and not look to the right or the left of the track. She searched only in the two directions of a straight line, which is far simpler than to search in all directions of the compass, as her ancestors must have done. For is not this deliberate search on either side of her nest analagous to the flight of orientation, commonly seen in the homing of bees and wasps? Is it not, in fact, itself a flight of orientation so simplified and so deliberately executed that we are able to follow each movement?

SETTING REACTIONS OF BIRD DOGS TO TURTLES

HAROLD C. BINGHAM

Several years ago an incident was reported to me regarding the setting response of a chicken dog to a snapping turtle. Mr. W. W. Azeltine, the reporter of the incident, was an experienced hunter and had had extensive experience with various types of dogs. His interesting account of the incident was recalled recently when, with a different dog, I observed a similar response.

In this note, I shall describe the two incidents that have come to my attention. They are significant, it seems, when one considers that both dogs were accustomed by nature and training to trail and "set" only warm blooded representatives of the higher vertebrates. In each of the incidents, the dog evidently confused the trail of a turtle with that of a prairie chicken. The habitual method of trailing and setting prairie chickens was characteristically adopted in response to the trail of a cold blooded vertebrate.

According to Mr. Azeltine's narrative, he was hunting with a mongrel, Prince, in which shepherd and setter blood apparently predominated. He had used the dog two seasons and in a section of the country where prairie chickens were abundant. The dog had had some experience with quail but, within the knowledge of the narrator, with no other species of this class of game birds. He regarded the dog as having an unusually reliable " nose."

While hunting on a fair day, Prince characteristically assumed, at the edge of a field of stubble, a solid setting posture. When encouraged to advance upon the expected game, the dog was unusually reluctant making the hunter look for a bird to flush at any moment. Prince, holding closely to the trail, was urged slowly across the field of stubble and into the long grass of a slough. At the end of the trail, he came upon a snapping turtle, from which he turned at once and began hunting.

After this experience, Prince was similarly fooled two or three times. Always he left the tortoise with indifference as soon as he reached the end of the trail.

The owner of an Irish setter reported to Mr. Azeltine similar experiences with his dog.

My own observation of this confusion of turtle and chicken trails occurred quite recently in the same section of the country, but prairie chickens had become scarce. I was hunting behind a yearling dog, Heinie, on the first day of the hunting season. I had owned the dog after he was approximately four months old. His ranging privileges had been rather restricted and only permitted under my own observation.

According to the fancier who sold Heinie, the male parent of the dog was a setter and the mother was a pointer. Heinie resembled the pointer stock, but his hunting was typically that of the setter. He relied chiefly upon trailing and, in comparison with other dogs I have used, his ability to locate game was rather inferior. In trailing, however, he was a moderately reliable young dog.

Heinie's first experience with prairie chickens came only a short time before his reaction to the trail of the land tortoise. In a field of stubble he had "set" quite satisfactorily a covey of chickens. Following the shooting, one of the escaped birds was being sought in the moderately high grass of an adjoining pasture. Heinie had been unable to locate it and we were leaving when he suddenly assumed the setting attitude. It was strikingly similar to his behavior not more than thirty minutes earlier and, despite the fact that we were some three or four hundred yards from the place where we had watched the chicken down, I thought he had located it. Obviously, Heinie was even more earnest and excited than in his previous reaction to the covey of chickens. He trembled characteristically and, as before, moved forward cautiously. So low did he crouch that at times his belly actually touched the ground. The direct trail that the dog seemed to be following made me suspicious and the outcome became even more doubtful when the distance reached something like one hundred yards. It was probably one hundred fifty yards before we came upon the maker of the trail—a sluggish land tortoise.

Upon reaching the animal, Heinie gradually relaxed from his tense setting attitude. In a half skulking response, he sniffed briefly and somewhat fearfully at the turtle, turned away abruptly, and went about his hunting apparently indifferent to his new acquaintance.